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The role of the seed-bank in the recovery of temperate heath and blanket bog following wildfires

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Nomenclature: Rose & O'Reilly (2006) for non-graminoid species; Poland & Clement (2009) for rushes and grasses; Jermy et al. (2007) for sedges; Council of the European Commission (1992) for habitats.

Abbreviations: Akaike Information Criterion adjusted for small sample size (AICc); Area of Special Scientific Interest (ASSI); European Forest Fire Information System (EFFIS); Generalised Linear Mixed Model (GLMM); partial Redundancy Analysis (pRDA); Northern Ireland Environment Agency (NIEA)

Abstract

Questions: Are the germinable seed-banks of upland heath and blanket bog reduced following wildfires? Are some species at particular risk? Do the impacts of wildfires on seed-banks differ between heathlands and blanket bog?

Location: Northern Ireland, United Kingdom

Methods: Vegetation surveys and seed-bank sampling were conducted in 2012 at burnt and unburnt areas within six upland sites where large wildfires had occurred during spring 2011. Differences in seedling abundance, species richness and Jaccard Similarity Indices between burnt and unburnt areas were compared using Generalised Linear Mixed Models (GLMMs). Differences in the community composition were examined using partial Redundancy Analysis (pRDA).

Results: 24 of the 51 species in the vegetation were detected in the germinable seed-bank. Species richness and the abundance of seedlings other than *Calluna vulgaris* were lower in areas where wildfires had occurred. Species composition of both germinable seed-banks and vegetation differed between burnt and unburnt areas within sites; with negative associations between burnt areas and some key indicator species including *Drosera rotundifolia*, *Eriophorum vaginatum* and *Empetrum nigrum*, *Narthecium ossifragum* and *Trichophorum germanicum*. We did not find any evidence of significant interactions between burning and habitat, suggesting that wildfires had similar impacts on each species regardless of the habitat in which they occurred.

Conclusions: This study differs from other UK studies in that it examines the impacts of wildfires at sites which have not been previously intensively managed by burning. In particular, we highlight potential impacts on *Narthecium ossifragum* and *Drosera rotundifolia* which are key components of the upland flora which to our knowledge were not present in previous UK studies.

Introduction

Wildfires play a major role in shaping ecosystems globally and are likely to become increasingly common in temperate regions less accustomed to this source of environmental stress as a result of climate change and increasing anthropogenic pressures (Krawchuk et al. 2009). Whilst climate change is predicted to increase precipitation and humidity overall in North-western Europe, seasonal variation in temperature and precipitation is likely to increase (Alcamo 2007). In particular, increased temperatures and decreased precipitation in summer months in the UK and Ireland (Blenkinsop & Fowler 2007; Murphy & Fealy 2010) may contribute to a greater frequency and intensity of uncontrolled fires (Albertson et al. 2011). European and UK wildfires are predominantly anthropogenic in origin with more than 95% of wildfires started by people (Birot et al. 2009; McMorrow et al. 2009). Thus, wildfires in the UK and Ireland represent an interaction between people, landscape and climate which may be mitigated by management actions.

Peatlands may be particularly vulnerable to changes in wildfire regimes, especially where management practices such as drainage, agriculture and peat-cutting have changed them from naturally fire resistant to fire prone ecosystems (Turetsky et al. 2014). Heathland and blanket bog are key upland habitats in northern Europe and support a unique flora and fauna of conservation interest (Thompson et al. 1995). Prescribed burning has been used to maintain open heathland habitats in Europe since Neolithic times, and has become increasingly common in the UK over the last 150-200 years where it is used to improve grazing for *Ovis aries*, *Cervus elaphus* and *Lagopus lagopus scoticus* (Thompson et al. 1995). Despite this, burning for conservation purposes remains controversial (Bradshaw et al. 2011), particularly on blanket bog where there is not enough evidence to predict its impacts on species of conservation concern (Stewart et al. 2005; Worrall et al. 2010). Specifically, some authors suggest that burning is likely to shift peatland habitats towards a drier state, and lead to the

51 decline of peat forming species such as *Sphagnum* and *Eriophorum* spp., whilst favouring the
52 establishment of *Calluna vulgaris* (Stewart et al. 2005; Littlewood et al. 2010; Bain et al.
53 2011). Contrary to these predictions, recent studies of prescribed burning have shown that a
54 10 year burning rotation favours peat-forming species when compared to reference plots
55 which had not been burnt for >87 years (Lee et al. 2013a) and that prescribed burning can
56 reduce the dominance of *C. vulgaris* and maximise species diversity on managed moorlands
57 (Harris et al. 2011).

58 Seed-banks play a key role in secondary succession and represent an important refuge for
59 plant species and source of future vegetation (Vandvik et al. 2016). However, some authors
60 suggest that seed-banks usually contain only a subset of the species present in vegetation, and
61 may be biased towards early successional species. Therefore, there is debate about the degree
62 to which seed-banks can be useful in the restoration of plant communities following
63 disturbance (Måren & Vandvik 2009). The similarity between seed-banks and vegetation
64 depends on the frequency of disturbance events, with plants in disturbed habitats (e.g.
65 anthropogenic heathland) investing more in sexual reproduction than in clonal growth,
66 resulting in a higher similarity between seed-banks and vegetation. Conversely, plants in less
67 disturbed habitats invest more in clonal growth and have greater disparity between vegetation
68 and seed-bank composition (Bossuyt & Honnay 2008; Klimešová & Herben 2015). Previous
69 studies of managed northern European heathlands have conformed to this expectation and
70 shown a strong correspondence between species in the vegetation and the seed-bank, with
71 65% of species in the vegetation detected in the seed-bank (Måren & Vandvik 2009).
72 However, studies of montane vegetation in Scotland found that, on average, only between 14
73 and 29% of species from the vegetation were detected in the seed-bank suggesting that the
74 seed-bank particularly in high altitude sites may be less suitable for habitat restoration (Miller
75 & Cummins 2003). However, similarity between seed-banks and vegetation in terms of

76 species overlap is highly dependent on seed-bank sampling area, with overlap increasing as
77 sampling effort increases making it difficult to compare results from different studies (see
78 Vandvik et al. 2016).

79 Studies of the response of seed-banks and vegetation to prescribed burning in north-
80 western European uplands have focused mainly on heathland rather than blanket bog sites
81 (e.g. Måren & Vandvik 2009), while others have been conducted on highly disturbed sites
82 with a previously reduced plant community (e.g. Lee et al. 2013a, b; Harris et al. 2011).
83 Whilst these studies provide useful information for the management of these sites, further
84 studies which examine a wider range of plant species are still needed (Bargmann et al. 2014).
85 This is particularly relevant in ecosystems which have not been subjected to frequent burning
86 in the past and where fire frequency may increase in the future through a combination of
87 climate change and anthropogenic influences.

88 Wildfires differ from prescribed burns in terms of their intensity and size, and few studies
89 have examined their impacts on temperate seed-banks. Experimental studies have found
90 minimal changes in temperature at depths of more than 1-2 cm below the soil surface in
91 prescribed fires (Davies et al. 2010; Ruprecht et al. 2013) but temperature changes during
92 wildfires may be greater (Turetsky et al. 2014). The aim of a prescribed burn is to remove
93 shrub vegetation whilst leaving moss, litter and soil layers intact and causing little change to
94 soil chemistry (Rosenburgh et al. 2013); although in practice loss varies from *ca.* 30-100%
95 vegetation, depending on a variety of factors including weather, topography and management
96 practice (Worrall et al. 2010). Conversely, uncontrolled wildfires frequently remove almost
97 all surface vegetation and alter soil structure and topography. Hence, they may cause greater
98 damage to both vegetation and seed-banks, particularly on blanket bog sites where
99 smouldering fires penetrate deeper into the soil (Turetsky et al. 2014).

100 In this study we focused on the impact of wildfires on the viability of seed-banks sampled
101 at six upland sites which have a broad plant flora representative of wet and dry heathlands
102 and blanket bog sites. Standing vegetation and seed-bank data were collected from burnt and
103 unburnt areas within each site, in order to examine the impacts of wildfires on germinable
104 seed-banks and the role of seed-banks in the recovery of vegetation. Specifically, we
105 hypothesised that: i) abundance and richness of the germinable seed-bank would be
106 significantly lower 1.0 - 1.5 years post-wildfire; ii) that wildfires would have different effects
107 on different species leading to changes in community composition of both the vegetation and
108 germinable seed-bank; iii) that the community composition of vegetation and the germinable
109 seed-bank would be more similar post-wildfire due to the germination of gap dependent and
110 fire adapted species from the seed-bank; and, iv) that impacts on blanket bog seed-banks
111 would be more severe than on the seed-banks of either dry or wet heath habitats.

112 **Methods**

113

114 **Study sites**

115 Samples were collected from burnt and unburnt areas within six upland sites in Northern
116 Ireland where large wildfires occurred in April 2011 (Fig. 1). The location and size of these
117 fires was derived from satellite data using the European Forest Fire Information System
118 (EFFIS, http://effis.jrc.ec.europa.eu). GIS mapping was used to identify six Areas of Special
119 Scientific Interest (ASSIs) within which large wildfires had occurred for inclusion in this
120 study. Information from pre-fire condition assessments, conducted by the Northern Ireland
121 Environment Agency (NIEA), Department of Environment (DOE) was used to classify
122 quadrats into three EU Annex I habitat classes using the Joint Nature Conservation
123 Committee (JNCC) National Vegetation Classification (NVC) system for UK habitats
124 (following Averis et al. 2004). Annex I habitats included were "blanket bog" (n=75),
125 "Northern Atlantic wet heaths with *Erica tetralix*" (n=25) and "European dry heaths" (n=22).
126 A total of 122 quadrats (2 x 2 m) were selected randomly from the quadrats which had been
127 previously surveyed by the NIEA for inclusion in this study. 71 quadrats were in areas burnt
128 during 2011 and 51 in nearby unburnt areas, such that burnt and unburnt areas were sampled
129 within each site. The unequal number of burnt and unburnt sites resulted from a discrepancy
130 between satellite images of burnt areas and actual field conditions. However, this sampling
131 design is adequate for the Generalised Linear Mixed Modelling approach taken in our
132 statistical analyses. The number of quadrats within each habitat was determined in proportion
133 to the occurrence of that habitat at each site. The mean distance between quadrats within sites
134 was 1.77 km (min = 0.07 km, max = 6.07 km). Details of site locations, habitats, fire size and
135 dates of burning are shown in supplementary material, Appendix 1.

136

137 **Seed-banks and vegetation**

138 Vegetation surveys and seed-bank sampling were conducted between 23rd June 2012 and
139 12th October 2012 (i.e. 14-18 months post-fire). The percentage cover of all vascular plant
140 species was assessed in each quadrat. All quadrats were surveyed by the same botanist for
141 consistency of evaluation. Seed-bank samples were taken using a cylindrical soil sampler
142 (5 cm in depth and 6 cm in diameter) at three locations 1 m apart within each quadrat. This
143 sampling regime accounted for potential aggregation of seeds on small spatial scales by
144 taking multiple samples within quadrats and optimised efficiency by only sampling the top
145 5 cm of soil where most viable seeds occur (Putwain & Gillham 1990; Pywell et al. 1997).
146 Soil samples were refrigerated between (2-5 °C) over-winter until the following April.
147 Individual soil samples for seed-bank germination were not aggregated within quadrats.

148 To maximise germination, seed-bank samples were concentrated by passing soil through
149 4 mm and 0.250 mm mesh width sieves to remove large material and fine particulate matter
150 (following Ter Heerdt et al. 1996). Seedling germination trials were initiated between the 8th
151 and 16th of April 2013 by spreading individual soil samples on top of ericaceous compost
152 (70% peat). An additional 60 control samples of pure compost were potted making a total of
153 426 samples (i.e. 60 control samples + 366 experimental samples; 3 samples from each of
154 122 quadrats). Sample pots were 7.5 cm in depth and sufficient compost was used such that
155 the soil samples were level with the top of the pots. Pots were placed in trays with 1 cm
156 depth of water to maintain adequate water supply, these were checked daily and manually
157 watered from above as required. The positions of burnt, unburnt and control samples was
158 randomly mixed, and changed twice weekly to reduce potentially confounding position
159 effects on germination. Seed-bank samples were germinated and grown under ambient light
160 conditions in an unheated greenhouse for a period of 15 weeks after which all seedlings were
161 identified, enumerated and removed. Soil samples were then vernalized by freezing at -20 °C

for 7 days and returned to the greenhouse for germination. Seedlings which emerged following vernalisation were identified and enumerated after a further 10 week growing period. A total of three seeds germinated in the 60 control pots (horticultural compost only) indicating that contamination of the seed-bank samples was likely to be very low. Therefore, data from the control pots were excluded from further analysis and no further adjustments were made to the dataset to control for contamination. Nomenclature follows Rose & O'Reilly (2006) for non-graminoid species; Poland & Clement (2009) for rushes and grasses; and Jermy et al. (2007) for sedges. Hence *Trichophorum germanicum* is used for the common species "deergrass" which is often referred to by earlier authors as *Trichophorum cespitosum*.

Soil chemistry

Five soil samples were taken at a minimum distance of 1 m apart for soil chemistry analysis within the same quadrats sampled for vegetation and the seed-bank between 3rd October 2012 and 5th November 2012. Soil samples for chemical analysis were combined to provide one soil sample for each quadrat which was analysed for pH, total nitrogen (%) and available phosphorus (mg/l) by the Agri-Food and Biosciences Institute (AFBI), Northern Ireland. pH was measured using a Skalar SP10 Robotic Analyser, total nitrogen using a TruMac® CN analyser and available phosphorus using a Skalar San Plus Auto Analyser.

Statistical analysis

Seed-banks

Differences in total seedling abundance, abundance of seedlings other than *C. vulgaris* and seedling species richness between samples from burnt and unburnt plots were assessed using

187 Generalised Linear Mixed Models (GLMMs). This approach was chosen as most appropriate
188 due to the non-normal distribution of the data and the spatially nested survey design (Bolker
189 et al. 2009; Grueber et al. 2011). An Information Theoretic modelling approach was used to
190 compare competing models. All possible variable subsets of the global model were fitted and
191 compared based on Akaike Information Criterion adjusted for small sample size (AICc).
192 Model averaging was used to estimate the relative importance and estimated effect size of
193 predictor variables from models within 2 ΔAICc of the model with the lowest AICc value
194 (hereafter, referred to as the 'best model'). Model-averaging was used as it is more reliable
195 than model selection procedures which rely on a single best model (e.g. stepwise selection
196 and minimum adequate model approaches) in cases where models have similar levels of
197 support as indicated by model Akaike weights (Burnham & Anderson, 2004; Johnson &
198 Omland, 2004). Specifically, model averaging is strongly advocated in cases where support
199 for the best model is <0.90, which was the case for all of our best models (Grueber et al.
200 2011). This situation can arise as a result of inherent collinearity between environmental
201 variables as is common in ecological field studies. Model averaging approaches are robust to
202 moderate levels of collinearity in explanatory variables and reduce the likelihood of
203 overestimating the effect of individual variables when compared to other model selection
204 procedures (Freckleton et al. 2011). Effect sizes of averaged models were estimated using the
205 zero method of model averaging; meaning that effect sizes were averaged across all models
206 with a value of zero in models in which they did not occur. This provides a conservative
207 estimate of the effect sizes of variables which occur in only a small proportion of models
208 within the best model set (Burnham & Anderson 2002).
209 Explanatory variables were chosen for inclusion in the initial global model based on their
210 importance in determining upland vegetation patterns, and therefore, their expected
211 usefulness in explaining the abundance and richness of germinable seed-bank species in this

212 study (Thompson et al. 1995; De Graaf et al. 2009). Topographical variables (i.e. Altitude
213 and Slope) were extracted from GIS raster files at a 25m resolution. Heat Load was a
214 measure of local temperature resulting from solar radiation, slope and aspect specifically
215 designed for use in vegetation science (McCune & Dylan, 2002). Here, the Heat Load Index
216 was calculated according to Equation 3 in McCune & Dylan (2002) based on raster data at a
217 25 m resolution. This equation was chosen as it was most suitable for areas with slopes of
218 less than 60º and latitudes of between 30-60º. Whilst this metric does not account for small-
219 scale variation in temperature caused by, for example, local shading or surface reflectance, it
220 provides a useful measure of differences in thermal environments at a landscape scale (e.g.
221 between north and south facing, or shallow and steep slopes). Soil variables (i.e. available
222 phosphorous, pH and total nitrogen) were checked for multicollinearity prior to inclusion in
223 models. These three soil variables showed low levels of correlation (Spearman's Rho > - 0.5
224 and < 0.5 in all cases), and, therefore, all 3 were included in the analysis. Grazing intensity
225 levels were assessed at each quadrat based on the quantity of dung present in each quadrat
226 and was ranked on a five-level ordinal factor scale of None < Rare < Occasional < Frequent <
227 Abundant. Specifically, Rare = 1-2 droppings, Occasional = 3-10, Frequent = 11-20,
228 Abundant > 20.

229 Initially, a global model was constructed including the explanatory variables "Burning"
230 (burnt or unburnt), "Habitat" (blanket bog, dry heath or wet heath), "Altitude" (m), "Slope" (º
231 from horizontal), "Heat load Index", "Julian day", "pH", "Available phosphorous" (mg^{-1}),
232 "Total Nitrogen" (mg^{-1}) and "Grazing". The interactions between "Burning*Grazing",
233 "Burning*Habitat" and "Burning*Slope" were also fitted to account for potentially different
234 impacts of burning in different contexts. Three level interactions were not included, due to
235 the insufficient sample sizes within some three-way interaction groupings. All explanatory
236 variables were rescaled to units of standard deviation prior to model fitting. "Quadrat" nested

within "Site" were fitted as random factors to account for variation explained by replication within quadrats and of quadrats within sites. Models were initially fitted using a Gaussian response distribution. Where model residuals were not normally distributed (based on a Shapiro-Wilk test), models were refitted by Laplace estimation with a Poisson and a negative binomial distribution (both with log link functions) and the optimal distribution was chosen based on the lowest AICc.

Similarity between germinable seed-banks and vegetation

Jaccard's Similarity Index was used to assess the similarity between seed-banks and vegetation in burnt and unburnt plots. The Jaccard Similarity represents the(proportion of shared species relative to the total number of species, and ranges from 0 (no shared species) to 1 (all species shared). It was chosen because it is based only on the presence/absence of species and not species abundances, hence, avoiding the conceptual issues which arise from comparing percentage cover in the vegetation and frequency in the germinable seed-bank. Prior to the calculation of Jaccard Similarity Indices between vegetation and the germinable seed-bank, seed-bank samples within each quadrat were combined so that they were on the same spatial scale as the vegetation. However, it should be noted that due to the different sample sizes within each quadrat (i.e. 4 m^2 for vegetation vs. 0.01 m^2 for the seed-bank) species present in the seed-bank at low abundances may not have been sampled. Nevertheless, the total volume of soil sampled for seed-bank analysis across sites (51,170 cm^3) should have been sufficient to estimate the relative frequency of most taxa in the seed-bank based on previous estimates of minimum sample volume for seed-bank studies which has varied from *ca.* 500 cm^3 in transient grasslands to *ca.* 50,000 cm^3 in late successional forests (Csontos 2007). Factors affecting the Jaccard Similarity between the

vegetation and the seed-bank were assessed using the same fixed factors, variables, GLMM approach and model averaging as described above. "Site" was fitted as a random factor.

Species composition of seed-banks and vegetation

Differences in plant community composition of seed-banks and vegetation were each assessed separately using partial Redundancy Analysis (pRDA). The species matrices were transformed using a Hellinger transformation prior to analysis. This transformation is appropriate for both percentage cover (i.e. vegetation data) and frequency data (i.e. seed-bank) (Legendre & Gallagher, 2001). Pre-transformation of species data followed by Euclidean-based RDA is a powerful statistical method for testing the relationship between environmental variables and species community data, which is robust to the presence of rare species and long environment gradients (Legendre & Gallagher, 2001). Partial RDA analysis was used to account for differences between sites, hence allowing for the interpretation of other environmental influences whilst the effect of "Site" was held constant (Bocard et al. 2011). Species matrices for seed-bank species were the number of seedlings of each species per quadrat. Species matrices for vegetation were the % cover of each species per quadrat and % other representing space not occupied by vascular plants (i.e. cover of non-vascular plants and bare ground). Explanatory variables in the global model pRDAs were the same as those described above in GLMM modelling. Explanatory variables were rescaled to units of standard deviation prior to model fitting. Model selection was conducted by forward step-wise selection from a null model containing only "Site" as a conditional variable. In each step, the variable from the global model which most significantly improved the model fit was added to the model based on pseudo-F statistics resulting from Monte Carlo permutations of the dataset (n permutations = 999). This process continued until no further variables improved the model fit significantly at a cut-off of $p = 0.05$. This is the most commonly used

method of model selection in RDA analyses (Bocard et al 2011). Significance of pRDA models and explanatory variables were calculated by Monte Carlo permutation with residuals of the species matrix permuted after accounting for variation within sites by pRDA (i.e. "reduced" method). This was computed using the function "anova.cca" in the package "vegan" in R where *n* permutations = 999 (Legendre et al. 2011). Significance of individual variables is given as marginal terms (i.e. each term was evaluated as the last term added to the model).

Mean values and confidence intervals in results and figures were calculated by non parametric bootstrapping of the raw data values, 95% confidence intervals are calculated by the bias corrected accelerated percentile method (BCa) suitable for non-parametric data (Crawley, 2013). All analyses were conducted using R 3.1.1. GLMMs were fitted using the packages "glmmabmb" (Fournier et al. 2012, vr. 0.7.7) and "MuMIn" (Barton 2013, vr. 1.9.11). Bootstrapping was conducted using the package "boot" (Canty & Ripley 2014, vr. 1.3-11). Jaccard's Similarity and pRDA were calculated in the package "vegan" (Oksanen et al. 2013, vr. 2.0-9).

Results

A total of 53 vascular plant species were present in the vegetation and 26 germinated from the seed-bank. Only two species in the germinable seed-bank were not present in the vegetation, *Juncus bufonius* and *Sagina procumbens*. Twenty-four species were common to both the germinable seed-bank and vegetation.

All 26 plant species that emerged from seed-bank soil samples, germinated prior to vernalisation by freezing. In total, 6,369 seeds geminated. The most commonly occurring species in the seed-bank were *C. vulgaris* (present in 98% of quadrats), *Erica tetralix* (62.3%) and *Erica cinerea* (34%). The most common species in vegetation were *C. vulgaris* (94% of quadrats), *E. tetralix* (61%) and *Eriophorum vaginatum* (57%). Species richness and most commonly occurring species in the vegetation and germinable seed-bank in each habitat type are shown in Table 1. For full list of species occurrences in vegetation and seed-bank (see supplementary material, appendix 3).

Seed-banks

Germinable seed abundance in the seed-bank was not significantly affected by burning, median seedling density in unburnt areas was 5,423 m^{-2} (mean = 6,994 m^{-2}, 95% confidence = 5,889 – 8,710 m^{-2}) compared to burnt areas with 5,069 m^{-2} (mean = 5,662 m^{-2}, 95% confidence = 4,981 – 6,714 m^{-2}; Fig. 2). The most important variable associated with total germinable seed abundance was slope, with which it was significantly negatively associated (Table 2a).

Seedling abundance of species other than *C. vulgaris* was negatively associated with burning with a median seedling density in unburnt areas of 1,297 m^{-2} (mean = 3,567 m^{-2}, 95% confidence = 2,598 - 5466 m^{-2}) and substantially reduced densities in burnt areas of 1,178m^{-2}

(mean = 1,802 m^{-2}, 95% confidence = 1,490 – 2,168 m^{-2}; Fig. 2). Non-*C. vulgaris* seedling abundance was significantly negatively associated with altitude (Table 2b).

Burning and slope were the most important variables associated with the species richness of the germinable seed-bank (as indicated by their inclusion in all models within 2 ΔAICc units of the best model). However, this result should be interpreted with caution as *p*-values were borderline for the effect of burning (β = -0.163 ± 0.080, p = 0.042). Burning was negatively associated with mean species richness, with a median richness of 2 species/sample in unburnt areas (mean = 2.4, 95% confidence = 2.2 – 2.6) compared to 2 species/sample in burnt areas (mean = 2.1, 95% confidence = 1.9 – 2.3; Fig 2.). Seedling species richness was significantly positively associated with slope (Table 2c).

Similarity between germinable seed-banks and vegetation

In total, 24 of 51 (47%) species present in the vegetation were detected in the germinable seed-bank. Notably some species characteristic of wet heath or blanket bog which were common in the vegetation were absent or rare in the germinable seed-bank e.g. *Eriophorum angustifolium, E. nigrum*, *Narthecium ossifragum*, *T. germanicum* and *Vaccinium myrtillus*. Whilst *Juncus bulbosus* and *Juncus effusus* were much more common in the germinable seed-bank than vegetation (Appendix 3).

The Jaccard Similarity between germinable species in the seed-bank and vegetation differed between habitat types and was significantly higher in dry heath (mean = 0.33, 95% confidence = 0.27 – 0.39) and blanket bog (mean = 0.33, 95% confidence = 0.30 – 0.36) than in wet heath (mean = 0.23, 95% confidence = 0.19 – 0.27) where β = 0.117 ± 0.038, p = 0.002 and β = 0.114 ± 0.037, p = 0.002 respectively). Dry heath and blanket bog did not differ in terms of Jaccard Similarity (β = 0.003 ± 0.038, p = 0.938). Areas with steeper slopes had a greater similarity between vegetation and germinable seed-banks although this

association was marginal (β = 0.054 ± 0.027, p = 0.046). A marginal interaction between burning and slope was also evident such that germinable seed-banks were less similar on steeper burnt plots (β = -0.059 ± 0.029, p = 0.044; Table 2d).

Species composition of germinable seed-banks and vegetation

The community composition of both the germinable seed-bank and vegetation differed significantly between burnt and unburnt areas (pseudo-F = 2.004, p = 0.010 and pseudo-F = 3.485, p = 0.005 respectively) based on pRDA analyses. The best model for germinable seed-bank composition included burning, habitat, soil pH and available phosphorus and explained explained 10.6% of the variation in seed-bank community composition after accounting for variance between sites (pseudo-$F_{df = 5,111}$ =3.057, p = 0.001; Table 3a and Fig 3a). The best model for vegetation cover included altitude, burning, habitat, heat load, soil pH and available phosphorus and explained 16.2% of the variation in the vegetation community after accounting for variance between sites (pseudo-$F_{df = 7,109}$ = 3.485, p = 0.005, Table 3b, Fig 3b).

In the germinable seed-bank only *E. tetralix* and *C. vulgaris* showed increased germination in soil samples from burnt areas, whilst the majority of other species present in the germinable seed-bank including sedge, rush and grass species showed a negative association with burnt areas (Fig. 3a).

In the vegetation, many species showed a positive association with burnt areas, including many sedges, rushes, grasses, herbs e.g. *Galium saxatile* and *Polygala serpyllifolia* and shrub species (*E. cinerea* and *V. myrtillus*), suggesting that the decline of these species in the germinable seed-bank may correspond with *in-situ* germination post-fire prior to our sampling. Only 3 species which were negatively associated with burning in the seed-bank did not show a positive association with burning in the vegetation surveys, namely: *J. bulbosus*, *J. effusus* and *E. vaginatum*. Conversely, some species were reduced in the vegetation post-

375 burning, namely: *C. vulgaris, Drosera rotundifolia, T. germanicum, N. ossifragum, E.*
376 *tetralix, E. nigrum* and *Molinia caerulea* (Fig. 3b). Four of these seven species (*D.*
377 *rotunifolia, E. nigrum, N. ossifragum* and *T. germanicum*) were rare in the germinable seed-
378 bank (i.e. detected in <1% of quadrats; Appendix 3).
379
380 **Discussion**
381 Our findings suggest that seed-banks in these sites of conservation concern had a lower
382 abundance of non-*Calluna vulgaris* species and species richness following wildfires. Similar
383 to previous studies, we found that the total abundance of germinating seed was not reduced
384 following recent burning, probably due to the increased germination of the most common
385 species, *C. vulgaris* and *E. tetralix,* which have been previously shown to increase in
386 germination post-fire (Bargmann et al. 2014; Vandvik et al. 2014). The majority of species
387 which declined in the germinable seed-bank increased in the post-fire vegetation, suggesting
388 that these germinated from the seed-bank post-fire and prior to our sampling as would be
389 expected in secondary successional dynamics. Notably, some species did not show this
390 pattern including *E. vaginatum* (which declined in the seed-bank and did not increase in the
391 vegetation) and *D. rotundifolia, E. nigrum, N. ossifragum* and *T. germanicum* (which
392 declined in the vegetation and were very rare in the seed-bank). These five species are
393 indicators of "favourable condition" in blanket bog and wet heath habitats in the UK (JNCC,
394 2006) and, therefore, important in maintaining the status of these habitats under the EU
395 Habitats Directive (Council of the European Commission, 1992).
396 As expected, other environmental factors were also very important in determining
397 germinable seed-bank abundance, richness and composition. In particular, steeper slopes had
398 a lower abundance and higher richness of germinable seeds, whilst the abundance of non-
399 *Calluna* species was lower at higher altitudes. Acidity and nutrient levels strongly influence

400 the species composition of Northern European moorlands (De Graaf et al. 2009) and these
401 associations were reflected in our dataset with pH and phosphorus availability being
402 associated with differences in species composition of both the germinable seed-bank and
403 vegetation. As expected, altitude and heat load were also associated with differences in
404 community composition of the vegetation, although these were less important than pH and
405 phosphorus. The total amount of variance in plant communities accounted for by
406 environmental variables, after accounting for differences between sites (10.6% in germinable
407 seed-banks and 16.2% in vegetation) were similar to those explained by environmental
408 variables in similar habitat types using multivariate techniques (e.g. Vandvik et al. 2005;
409 Harris et al. 2011) and to that which can be explained by many other ecological studies
410 (Møller & Jennions 2002). High levels of unexplained residual variance in these species
411 communities may indicate a strong role of stochasticity in species assembly and/or the effects
412 of environmental variables not accounted for here.

413 We hypothesised that impacts on blanket-bog would be more severe than those in
414 heathland habitats due to the potential for smouldering burns of longer duration. However,
415 we found no evidence of significant interactions between burning and habitat in any of our
416 models suggesting that wildfires had similar impacts on each species regardless of the habitat
417 in which the species occurred. Despite this, pRDA analysis highlighted declines in key
418 indicator species of blanket-bog and wet heath (*D. rotundifolia, E. nigrum, N. ossifragum* and
419 *T. germanicum*) suggesting that some species in those habitats may be at higher risk.

420 These results indicate some support for the suggestion by Littlewood et al. 2010 that
421 burning (in this case by wildfires) may reduce the prevalence of peatland specialist species
422 and should be avoided if "favourable condition" is to be maintained (Stewart et al. 2005).
423 However, our results need to be put in the context of successional dynamics and previous
424 studies. Two of the aforementioned species, *E. vaginatum* and *T. germanicum*, have been

425 suggested to have positive associations with burning management (Preston et al. 2002) and in
426 particular *E. vaginatum* has been shown to have higher abundance in areas with a 10 year
427 management burning rotation than in areas which have been unburnt for >87 years. Both
428 species have low occurrence in persistent seed-banks (Miller and Cummins 2003; Måren &
429 Vandvik 2009) and are capable of clonal regeneration by rhizomes both above and below
430 ground (Klimešová & de Bello 2009). The observed contrast between the negative
431 associations shown here and previous studies may be due to the higher temperatures and
432 durations of wildfires relative to prescribed burning and/or to differences in the time-frame
433 between studies.

434 *N. ossifragum, E. nigrum* and *D. rotundifolia* are less common in upland vegetation than
435 *E. vaginatum* and *T. germanicum* (present in 21%, 10%, 4%, 57% and 43% of vegetation
436 quadrats respectively in this study). Reproduction of *N. ossifragum* is primarily clonal from
437 both above and below ground rhizomes and bud-banks (Summerfield 1974; Klimešová & de
438 Bello 2009; Tsaliki & Diekmann 2009). Sensitivity to fires has been previously suggested in
439 *N. ossifragum* at UK sites (Summerfield, 1974), although to our knowledge this has not been
440 shown empirically. *N. ossifragum* is associated with late successional vegetation, *ca.* 20 years
441 after prescribed fires, in Scandinavian heathlands indicating the potential for recovery in the
442 later stages of succession (Måren & Vandvik, 2009). Populations of this species in the UK
443 appear stable over last 20 years but the species is of concern as it shows high habitat
444 specificity and is likely to require stable habitat conditions for population stability (Tsaliki &
445 Diekmann, 2009).

446 *E. nigrum* is a low growing shrub species which was similarly rare in other studies of
447 upland seed-banks (eg. Miller & Cummins 2003; Måren & Vandvik 2009). This may be due
448 in part to poor germination, as this species shows deep dormancy and may require multiple
449 cold stratifications and/or higher germination temperatures (Bell & Tallis 1973; Graae et al.

2008). Vegetative reproduction by *E. nigrum* is by rhizomes and resprouting at or above soil level rather than below-ground (Klimešová & de Bello, 2009) making it more likely for these to be damaged by severe fires. Results from previous UK studies on prescribed burning of blanket bog in the UK have been equivocal with *E. nigrum* showing complex responses to combinations of grazing and burning (e.g. Lee et al. 2013a). However, two previous studies of shrubland and forest fires found no recovery of *E. nigrum* over periods of 4-5 years post-burning (Penney et al. 2007; Hekkala et al. 2014).

D. rotundifolia may be under-detected in the seed-bank in this study due to its low frequency in the vegetation, and, therefore, results should be treated with particular caution. *D. rotundifolia* is capable of sexual and asexual reproduction in peatland habitats (Hoyo & Tsuyuzaki 2015), and similarily to *E. nigrum* asexual reproduction is mostly at or above soil level, although in *D. rotundifolia* below-ground bud-banks may also be present (Klimešová & de Bello 2009). *Drosera* sp. are particularly dependent on mature rosettes for the maintanence of population sizes due to high mortality rates of seedlings (Nordbakken et al. 2004), and, therefore, may be particularly vulnerable to disturbances such as fire which can destroy large numbers of adult plants. However, given the low occurrence of this species in this study (present in 4% of quadrats) further species-specific research to quantify the effects of fire on its seed-banks and secondary succession are required.

In total, 47% of the species in the vegetation were detected in the seed-bank (24 of 51), suggesting that many species do not have large persistent seed-banks in these habitats. Due to the disparity between the sampling area of seed-banks and vegetation in this study (i.e. $4m^2$ quadrats in vegetation and $0.01m^2$ per quadrat in the seed-bank) it is likely that the estimated Jaccard Similarity Indices of germinable seed-banks and vegetation would be higher if larger seed-bank areas were sampled, since some species with a lower frequency of seeds would probably be detected (see Vandvik et al. 2016). Furthermore, as these Jaccard Similarity

475 Indices are calculated per quadrat for the purposes of GLMM analyses they are lower than
476 would be expected when calculated across all quadrats within each habitat type. For
477 comparison with previous studies similarity at this broader habitat scale was calculated as the
478 proportion of species in the vegetation which are also present in the seed-bank (Table 1).
479 Despite this, as sampling regimes were constant across areas within this study relative
480 differences in Jaccard Similarity (e.g. between habitats) are reliable.

481 Rapid germination of many species post-fire is likely, due to increased light and nutrient
482 availability, reduced competition and/or fire related cues such as smoke and temperature
483 (Bargmann et al. 2014; Snyman 2015). Therefore, we expected that in areas where wildfires
484 occurred, vegetation and seed-banks would be more similar; however, we did not find any
485 evidence to support this hypothesis. Furthermore, we found species such as *V. myrtillus* and
486 *Carex pilulifera* which were uncommon in the seed-bank became more common in the
487 vegetation post-fire. These species have clonal traits including below-ground bud-banks and
488 rhizomes (Klimešová & de Bello, 2009), which may also be important in post-fire recovery.
489 Germinable seed-banks and vegetation in steep areas were marginally less similar in burnt
490 areas. This may be due to a loss of germinable seed and/or seedlings on steep slopes after
491 wildfires due to altered abiotic conditions, such as increased erosion and extreme weather
492 conditions (Maltby et al. 1990).

493 All seed-bank studies are dependent on the sampling and germination methods employed.
494 Here, mean seed abundances per m^2 were at the lower end of the range of abundances found
495 in similar upland communities (Miller & Cummins 2003; Måren & Vandvik 2009), but were
496 similar to those found in upland bog habitats and European heaths (Lee et al. 2013b; Bossuyt
497 and Honnay 2008). Community composition detected in this study was similar to that found
498 by previous authors, with a dominance of *C. vulgaris* and *E. tetralix*, and an over-
499 representation of *Juncus* species in the germinable seed-bank relative to the vegetation

500 (Miller & Cummins 2003; Bossuyt & Honnay 2008; Måren & Vandvik 2009). Species which
501 were not detected in germinable seed-banks here include those with transient seed-banks
502 which would not be expected due to the timing of the sampling, and species which have
503 shown similarly low seedling abundances in previous studies such as *Vaccinium* sp. (Miller &
504 Cummins 2003; Måren & Vandvik 2009). Hence, the relative frequencies of species found in
505 this study are comparable with those of other studies in similar habitats and are, therefore,
506 considered by the authors to be suitable for comparing the relative frequencies of major
507 species in germinable seed-banks between burnt and unburnt areas. However, inevitably
508 some species with low germinable seed abundances and/or clumped distributions may have
509 been overlooked by the sampling regime employed.

510 Here, we focused on differences between sites over a short timeframe (14-18 months post-
511 fire) and, therefore, it was not possible to determine the long-term impacts of wildfires on
512 species communities. Further research is required to ascertain whether the differences in the
513 germinable seed-bank observed here are due to damage to the seed-bank or early post-fire
514 succession. This will have important implications for whether management interventions
515 such as reseeding or alterations to the abiotic environment are necessary for the re-
516 establishment of some key species post-wildfire.

517 The impact of fire on key peatland species may have been overlooked in previous studies
518 due to the overwhelming dominance of *C. vulgaris* in the seed bank, because of a focus on
519 sites with a history of regular burning for management, or on sites where species richness was
520 already low. In particular, we highlight the potential negative impacts on key indicator
521 species such as *N. ossifragum* and *D. rotundifolia* which are characteristic of wetter sites, and
522 which, to our knowledge, were not present in previous studies of moorland burning in the
523 UK. The absence of a focus on these species in previous studies may relate to shifting
524 baselines, where species composition post-disturbance is being compared to an already

525 reduced or altered species community. In addition, we found negative associations between
526 these wildfires and some key indicator species (T. *germanicum, E. vaginatum* and *E.*
527 *nigrum*), which have been found to be positively associated with prescribed burning in
528 previous UK studies. This may relate to the variable influence of burning at different sites,
529 differences between wildfires and prescribed burning and/or differences in timescales
530 between studies. In conclusion, this study provides evidence of the potential negative impacts
531 of wildfires on key indicator taxa and highlights the need for further studies on a more
532 diverse range of sites in order to quantify potential impacts on key species.

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Author contributions:

Research was designed by RK, WIM & NR. Data collection, greenhouse experiments and data analyses were conducted by RK. Manuscript was written by RK and edited by EB, WIM and NR.

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Supplementary material

Appendix 1. Table S1. Details of study site locations, characteristics and management (pdf format).
Appendix 2. Table S1. Details of study site locations, characteristics and management (csv format).
Appendix 3. Table S2. Relative frequency of species in vegetation and germinable seed-bank (pdf format).
Appendix 4. Table S2. Relative frequency of species in vegetation and germinable seed-bank (csv format).
Appendix 5. Germinable seed-bank dataset summarised at quadrat level (csv format).

Table 1. Comparison of seed-banks and vegetation in each habitat type, showing species richness, percentage of seed-bank species found in vegetation and the most commonly occurring species in each habitat type.

Habitat	**Species richness**		**% of vegetation species in seed-bank**	**Most common species (% of quadrats in which species is detected)**	
	Vegetation	Seed-bank		Vegetation	Seed-bank
Blanket bog	33	21	58%	*Calluna vulgaris* (99%) *Eriophorum vaginatum* (82%) *Erica tetralix* (62%)	*Calluna vulgaris* (99%) *Erica tetralix* (68%) *Juncus effusus* (21%)
Dry heath	35	19	40%	*Calluna vulgaris* (95%) *Erica cinerea* (81%) *Potentilla erecta* (77%)	*Calluna vulgaris* (100%) *Erica cinerea* (86%) *Carex binervis* (55%)
Wet heath	25	17	44%	*Molinia caerulea* (92%) *Erica tetralix* (84%) *Trichophorum germanicum* (80%) *Calluna vulgaris* (80%)	*Calluna vulgaris* (92%) *Erica tetralix* (68%) *Erica cinerea* (68%)

Table 2. Model averaged results of Generalised Linear Mixed Models (GLMMs) for **a)** germinable seed abundance, **b)** Non-*Calluna vulgaris* germinable seed abundance, **c)** germinable seed-bank richness and **d)** Jaccard Similarity of germinable seed-banks and vegetation. Explanatory variables are listed in descending order of importance based on their model averaged Akaike (AICc) weights ($\sum\omega_i$). Factorial comparisons of habitat types were given as "Habitat1/Habitat2" where the habitat after the "/" was the reference condition.

Model (response distribution) Explanatory variables	$\sum\omega_i$	β ± s.e.	Z value	*p*
a) Total germinable seed abundance (negative binomial)				
Slope	1.00	-0.253 ± 0.100	2.522	0.012
Altitude	0.94	-0.200 ± 0.109	1.838	0.066
Burning	0.49	-0.099 ± 0.145	0.685	0.493
Julian Date	0.37	-0.052 ± 0.091	0.564	0.573
Heat load	0.27	-0.020 ± 0.053	0.371	0.711
Grazing	0.11	-0.015 ± 0.069	0.219	0.827
Soil Nitrogen	0.06	-0.003 ± 0.023	0.125	0.901
Burning*Grazing	0.06	0.015 ± 0.074	0.201	0.841
b) Non-*Calluna vulgaris* germinable seed abundance (negative binomial)				
Altitude	1.00	-0.547 ± 0.131	4.158	<0.001
Burning	1.00	-0.523 ± 0.196	2.653	0.008
pH	0.94	0.217 ± 0.123	1.767	0.077
Slope	0.77	0.250 ± 0.223	1.118	0.264
Heat load	0.76	-0.142 ± 0.122	1.166	0.243
Julian date	0.39	0.070 ± 0.123	0.571	0.568
Burning*Slope	0.29	-0.081 ± 0.166	0.166	0.622
Soil phosphorus	0.18	0.017 ± 0.061	0.274	0.784
Soil nitrogen	0.12	0.012 ± 0.051	0.230	0.818
Grazing	0.12	-0.009 ± 0.047	0.196	0.845
c) Germinable seed-bank species richness (negative binomial)				
Burning	1.00	-0.163 ± 0.080	2.036	0.042
Slope	1.00	0.199 ± 0.078	2.535	0.011
Burning*Slope	0.91	-0.127 ± 0.081	1.568	0.117
Heat load	0.86	-0.060 ± 0.042	1.406	0.159
Habitat – Bog/Dry Heath	0.71	-0.196 ± 0.161	1.217	0.224
Habitat – Bog/Wet Heath	0.71	-0.186 ± 0.152	1.219	0.223
Habitat – Dry Heath/Wet Heath	0.71	0.011 ± 0.104	0.104	0.917
Altitude	0.65	-0.066 ± 0.067	0.988	0.323
Julian Date	0.39	0.028 ± 0.045	0.616	0.538
Soil nitrogen	0.29	-0.016 ± 0.035	0.457	0.648
Soil phosphorus	0.29	0.019 ± 0.039	0.481	0.631
Soil pH	0.11	0.004 ± 0.019	0.234	0.815
Grazing	0.06	-0.001 ± 0.011	0.112	0.911
d) Jaccard Similarity of germinable seed-banks and vegetation (Gaussian)				
Habitat – Bog/Dry Heath	1.00	-0.003 ± 0.038	0.077	0.938
Habitat – Bog/Wet Heath	1.00	0.114 ± 0.037	3.035	0.002
Habitat – Dry Heath/Wet Heath	1.00	0.117 ± 0.038	3.097	0.002
Julian Date	0.91	-0.025 ± 0.014	1.699	0.089
Burning	0.90	0.002 ± 0.021	0.100	0.921
Slope	0.90	0.054 ± 0.027	1.987	0.047
Burning*Slope	0.90	-0.059 ± 0.029	2.014	0.044
Soil pH	0.89	-0.023 ± 0.015	0.015	0.113
Altitude	0.44	-0.010 ± 0.015	0.692	0.489
Soil Phosphorus	0.27	-0.004 ± 0.009	0.448	0.654

Table 3. Partial Redundancy Analysis (pRDA) permutation test results of variables in best fitting model for **a)** species composition of germinable seed-bank and **b)** species composition of vegetation. Site was fitted as a conditional factor in all models. Constrained and conditional variances are given as the proportion of the total variance in each species community. 'Variance explained' is shown as the proportion of the total variance in the species community explained when a variable is fitted as the last term in the model (i.e. marginal terms). Explanatory variables are listed in descending order of importance based on the variance explained.

Model Explanatory variables	**DF**	***Explained variance* (%)**	**Pseudo-*F***	***P***
a) Germinable seed-bank (Constrained variance = 10.6 %, Conditional variance (Site) = 12.1%, residual df = 111, pseudo-F = 3.057, p = 0.001)				
Soil pH	1	5.1	7.350	0.005
Soil phosphorus	1	1.9	2.723	0.010
Burning	1	1.4	2.004	0.010
Habitat	2	2.1	1.510	0.060
b) Vegetation cover (Constrained variance = 16.2 %, Conditional variance (Site) = 11.3% , residual df = 109, pseudo-F = 3.485, p = 0.005)				
Soil pH	1	5.5	8.341	0.005
Habitat	2	3.6	2.684	0.005
Burning	1	2.5	3.687	0.005
Soil phosphorus	1	1.4	2.057	0.010
Altitude	1	1.1	1.713	0.017
Heat load	1	1.1	1.586	0.033

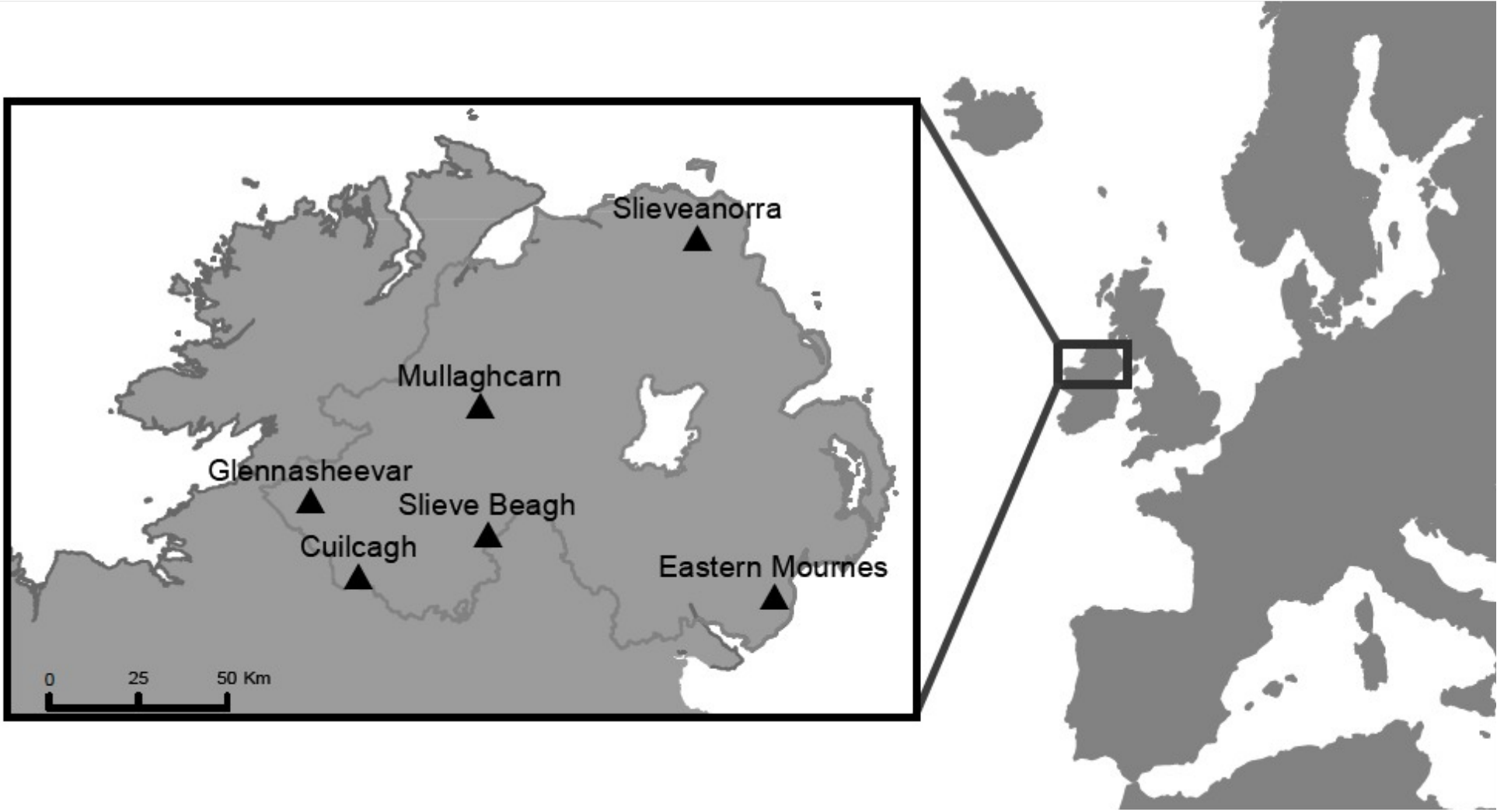

Fig. 1 Locations of field sites.

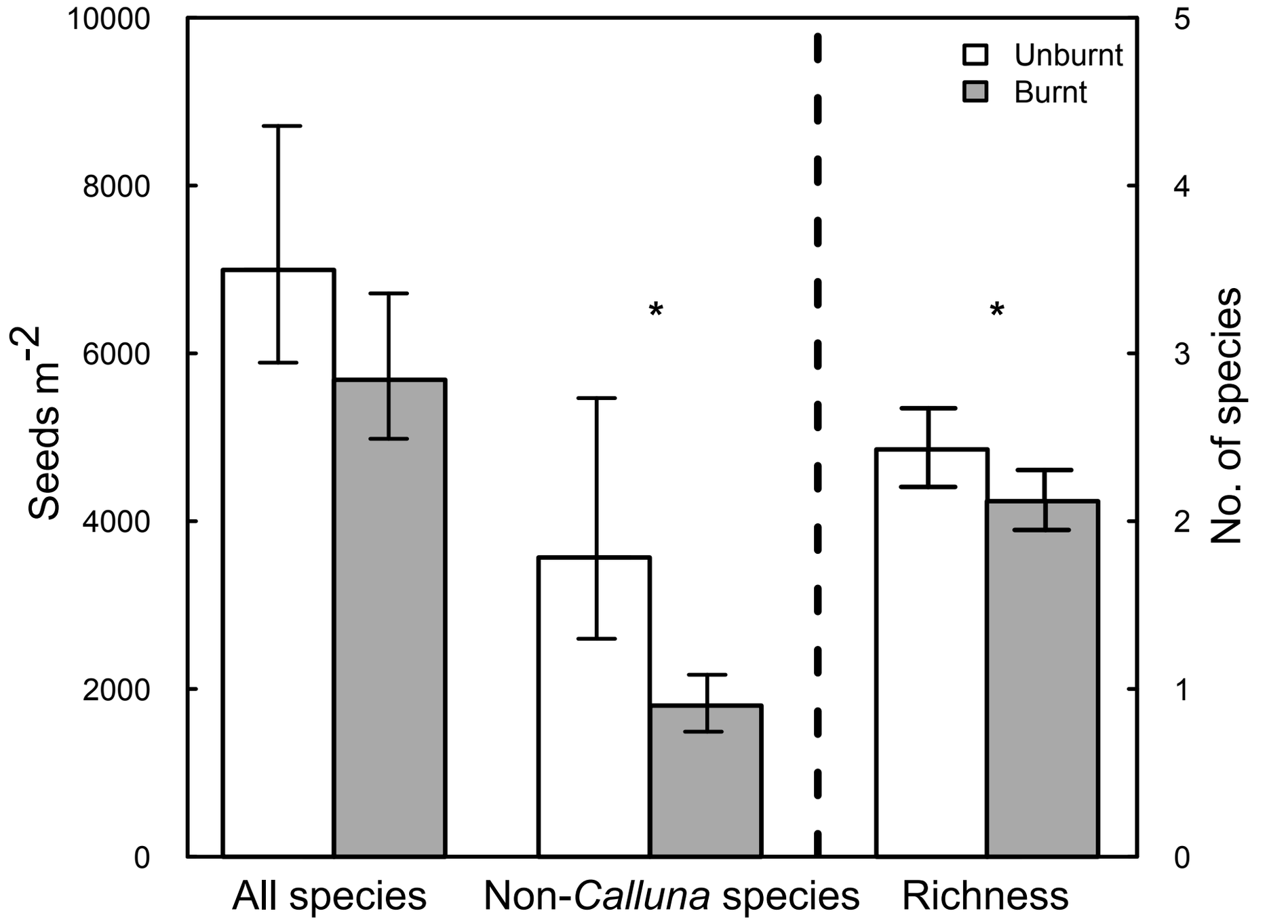

Fig. 2 Mean seed abundance per m^2 and mean species richness per sample in burnt and unburnt areas. Error bars show bootstrapped 95% confidence intervals on the mean. *'s indicate a significant difference between burnt and unburnt areas based on Generalised Linear Mixed Model outputs.

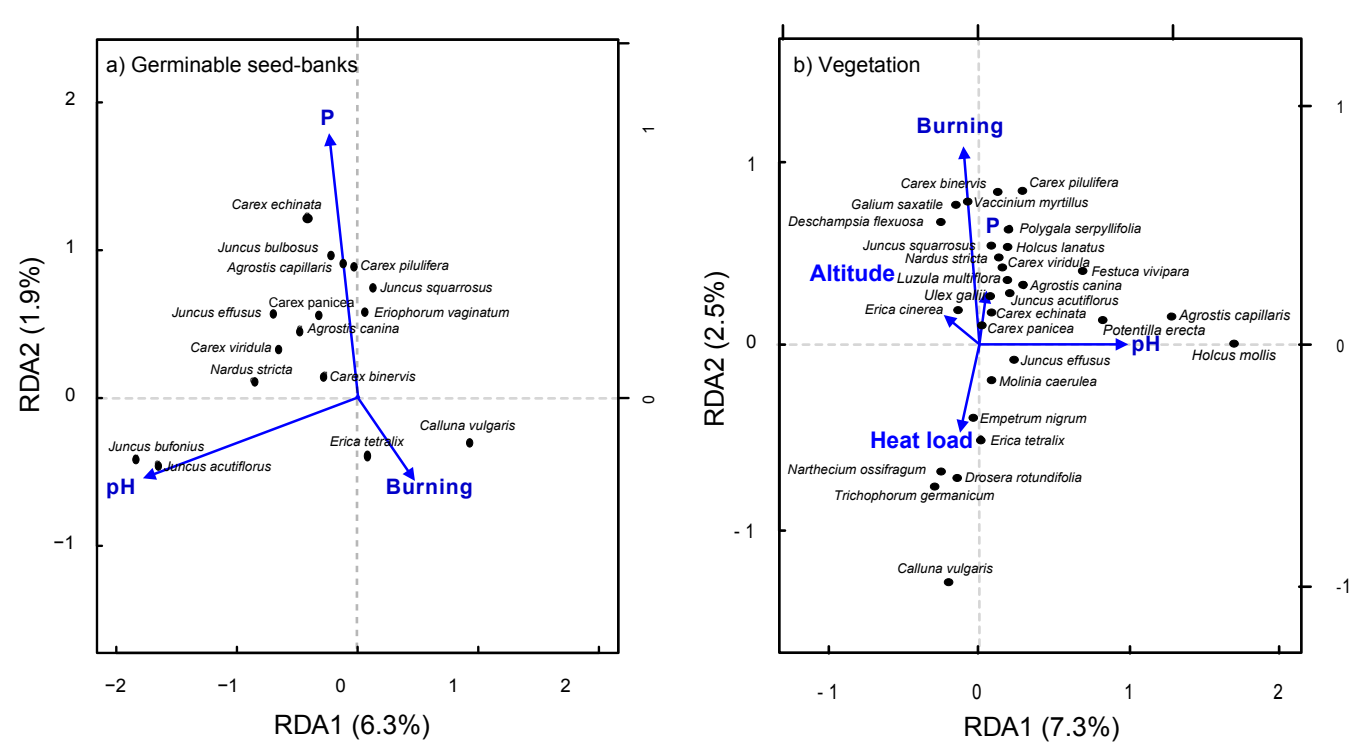

Fig. 3 Biplots showing the association between environmental variables and plant species composition. Species are plotted where they occur in more than 1 quadrat and more than 5% percent of the variation in their abundance is explained by the RDA model after differences between sites are accounted for.

Supporting information for the article

Kelly, R., Boston, E.M., Montgomery, W.I.M. & Reid.N. 2016. The role of the seed-bank in the recovery of temperate heath and blanket bog following wildfires. *Applied Vegetation Science.*

Table S1. Details of study site locations, characteristics and management. Habitats were classified into into classes using the JNCC National Vegetation Classification system for UK habitats. Annex I habitats included were "blanket bog" (*n*=75), "Northern Atlantic wet heaths with *Erica tetralix*" (*n*=25) and "European dry heaths" (*n*=22). Data on area and dates of wildfires were supplied by the European Forest Fire Information System – EFFIS (http://effis.jrc.ec.europa.eu) of the European Commission Joint Research Centre and are derived from MODIS satellite data.

Site/Area of Special Interest (ASSI's)	No. of quadrats	Latitude (WGS 1984)	Longitude (WGS 1984)	Altitude range (m)	pH range	EU Annex 1 Habitats	Management	Total area of wildfire (km^2)	Dates of fires
Cuilcagh	18	54.2354	-7.7498	198 - 396	3.9 – 5.8	Blanket bog, Dry Heath, Wet Heath	Low intensity cattle and sheep grazing	1.4	02/05/2011
Eastern Mournes	34	54.1655	-5.9620	202 - 554	4.0 – 4.8	Blanket bog, Dry Heath, Wet Heath	Low intensity sheep grazing/ recreational use (hill-walking)	9.9	10/04/2011 01/05/2011
Glennasheevar	11	54.4342	-7.9590	184 - 245	4.1 - 4.3	Blanket bog, Wet Heath	Low intensity sheep grazing	3.7	02/05/2011
Mullaghcarn	20	54.6783	-7.2176	218 - 505	3.9 – 4.2	Blanket bog, Dry Heath	Low intensity sheep grazing at 70% of site	12.0	23/04/2011 02/05/2011
Slieve Beagh	19	54.3411	-7.1926	241 - 352	3.9 – 4.2	Blanket bog	Low intensity sheep grazing at 66% of site	23.7	01/05/2011
Slieveanorra	20	55.1072	-6.2510	232 - 345	3.9 – 4.2	Blanket bog	Low intensity cattle grazing at 33% of site	1.1	22/04/2011

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Table S2. Relative frequency of species in vegetation and germinable seed-bank, showing percentage of quadrats in which species were detected. Species are ranked in order of frequency in the vegetation. Species recorded in 0% of quadrats are given as "not detected" to indicate that they may be present in low numbers but undetected.

Species	Percentage of quadrats (%)	
	Vegetation	Germinable seed-bank
Calluna vulgaris	94.3	97.5
Erica tetralix	61.5	62.3
Eriophorum vaginatum	57.4	4.9
Trichophorum germanicum	43.4	Not detected
Eriophorum angustifolium	41.0	0.8
Potentilla erecta	40.2	15.6
Molinia caerulea	39.3	2.5
Vaccinium myrtillus	39.3	Not detected
Erica cinerea	28.7	34.4
Narthecium ossifragum	21.3	Not detected
Deschampsia flexuosa	18.0	9.8
Carex pilulifera	16.4	5.7
Polygala serpyllifolia	13.9	Not detected
Agrostis canina	13.1	13.1
Nardus stricta	11.5	9.0
Empetrum nigrum	10.7	0.8
Galium saxatile	10.7	3.3
Agrostis capillaris	8.2	1.6
Carex panicea	8.2	1.6
Luzula multiflora	6.6	Not detected
Carex binervis	5.7	15.6
Ulex gallii	5.7	Not detected
Carex echinata	4.9	7.4
Drosera rotundifolia	4.1	0.8
Juncus squarrosus	3.3	4.9
Juncus effusus	3.3	23.0
Carex viridula	2.5	3.3
Carex nigra	2.5	Not detected
Juncus acutiflorus	1.6	1.6
Danthonia decumbens	1.6	Not detected
Festuca.vivipara	1.6	Not detected
Holcus lanatus	1.6	Not detected
Holcus mollis	1.6	Not detected
Myrica gale	1.6	Not detected
Epilobium palustre	0.8	3.3
Juncus bulbosus	0.8	23.0
Anthoxanthum odoratum	0.8	Not detected
Betula pubescens	0.8	Not detected
Carex rostrata	0.8	Not detected
Cirsium dissectum	0.8	Not detected
Drosera intermedia	0.8	Not detected
Juncus conglomeratus	0.8	Not detected
Listera cordata	0.8	Not detected
Oxalis acetosella	0.8	Not detected
Salix repens	0.8	Not detected
Schoenus nigricans	0.8	Not detected
Sorbus aucuparia	0.8	Not detected
Rumex acetosella	0.8	Not detected
Trifolium repens	0.8	Not detected
Vaccinium oxycoccos	0.8	Not detected
Viola riviana	0.8	Not detected
Sagina procumbens	Not detected	0.8
Juncus bufonius	Not detected	1.6